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Recruitment of Northern shrimp (*Pandalus borealis*) off West Greenland in Relation to Spawning Stock Size and Environmental Variation, 1993-2004

by

Kai Wieland

Greenland Institute of Natural Resources
Box 570, 3900 Nuuk, Greenland

Abstract

Standard and modified Ricker stock-recruitment functions incorporating environmental variables were compared in order to examine the effect of stock size, mean female size, predator biomass and temperature on recruitment at age 2 using female biomass corrected for the temperature-dependent of maturity and, alternatively, egg production as a measure of parental stock size.

The standard Ricker models represented the observed recruitment not very well. Much better fits were obtained when environmental variables were incorporated in the stock-recruitment relationship. In addition to parental stock size, significant variables were mean female length, bottom temperature in the year the larvae settled and biomass of Greenland halibut as a proxy for predation on the 1-group. The results suggest that recruitment will be at or even below average in the coming three years despite a high level of female biomass. This interpretation should, however, been taken with some caution as the analysis was based on a short time series.

Introduction

A transition from cold to warm conditions has been observed in West Greenland waters in the mid-1990s. In the same period recruitment of northern shrimp increased considerably and this was followed by an increase of stock biomass to a record high level (Wieland, in prep.). In the most recent years, however, recruitment was below what could have been expected from the high female biomass, and it has become questionable whether female biomass is an adequate measure of the reproductive potential of the stock. Related to the change towards a warmer environment, a substantial decline in length at sex transition was observed, and it has been argued that this could result in a lower population fecundity if not compensated otherwise, e.g. by a transition from bi-annual to annual spawning (Wieland, 2004a).

Material and Methods

Relationships between parental stock size (P) and recruitment (R) were fitted to the original Ricker model (Ricker, 1954):

$$R = a * P * \exp(-b * P)$$

where a and b are the coefficients of the density independent and the density-dependent term, respectively.

Alternatively, its linearized and extended version according to Stocker *et al.* (1985) was used:

$$\ln(R_i / P_{i-3}) = \ln(\alpha) - \beta * P_{i-3} + \chi * L_{i-3} + \delta * ST_{i-2} + \eta * BT_{i-2} + \lambda * C_{i-1} + \mu * G_{i-1}$$

where R is the recruitment at age 2, *P* is the biomass of mature females (or potential egg production), α and β are the coefficients of the two Ricker terms, *L* is the mean carapace length of the females, *ST* and *BT* are surface and bottom temperature, *C* and *G* are survey estimates of cod (*Gadus morhua*) and Greenland halibut (*Reinhardtius hippoglossoides*) biomass at West Greenland, *i* denotes year, and χ, δ, η, γ and μ are coefficients for the environmental variables. In this formulation the environmental effects are multiplicative as suggested by Ricker (1975), and non-significant variables were removed from the full model by backward stepwise multiple regression.

The lag of three years between female biomass and age 2 recruits takes into account that the females found in a summer survey produce offspring that emerges as larvae first in the following spring and as age 2 three years later. The surface and bottom temperatures, which have been recorded in summer, were lagged by two years so that they correspond to the year in which the larvae hatched and settled. Cod and Greenland halibut biomass were shifted two years back in time in order to reflect predation on northern shrimp in particular at age 1.

Information on average bottom temperature in the study area, recruitment at age 2 as well as female biomass and mean size (Fig. 1) were collected during the West Greenland Bottom Trawl survey for northern shrimp and the most recent descriptions of the methods used to compute the these time series are given in Wieland *et al.* (2004) and Wieland (2004b). Surface temperatures measured on a standard hydrographic station on Fyllas Bank were obtained from Ribergaard and Buch (2003) for the years 1990 to 2003 and from Ribergaard (pers. com.) for 2004. Survey estimates of cod and Greenland halibut biomass (Fig. 1) were available from ICES (2004) and Storr-Paulsen and Jørgensen (2004), respectively, for the period 1990 to 2003. For 2004, preliminary survey estimates of cod and Greenland halibut biomass from Storr-Paulsen and Wieland (2004) and from Storr-Paulsen (pers.com.) were included in the analysis.

Horsted (1978) summarized information on the spawning period of northern shrimp at West Greenland noting that not all females became ovigerous during winter of the same year and that the proportion of spawning females varied between about 20 and 90% in different areas and years, but no relationship with temperature could be established from his observations. Skúladóttir *et al.* (1991) reported that northern shrimp does not spawn every year in Iceland offshore waters whereas the proportion of egg bearing females during winter was almost 95% in inshore areas at higher temperatures. A second order polynomial regression was fitted to these data (Fig. 2) and was used to calculate the proportion of mature females in West Greenland waters for the years 1990 to 2004 (Fig. 3) based on the bottom temperatures observed there (Fig. 1). The original survey estimates of female biomass were then multiplied with the temperature-specific maturity proportion in order to obtain a time series of mature female biomass of northern shrimp off West Greenland.

Individual fecundity of northern shrimp depends on female size (e.g. Shumway 1985), but such data are very fragmentary for West Greenland waters (Horsted and Smidt, 1956; Folmer, 1990). Teigsmark (1983) provides fecundity length relationships for different parts of the Barents Sea, and the lower one was used here to estimate potential egg production (EP) of the northern shrimp population in West Greenland waters for years with a bottom temperature (T) below 2°C and the higher one was applied for the other years considering the observation of Berenboim (1982) that temperatures below 2°C lowered fecundity of northern shrimp in the Barents Sea, i.e.:

$$EP = N * \exp(-4.35 + 3.64 * \ln(L)) \qquad \text{if T < 2 °C (1990 – 1995) and}$$
$$EP = N * \exp(-3.78 + 3.52 * \ln(L)) \qquad \text{if T > 2 °C (1996 – 2004),}$$

where *N* is the abundance of mature females (calculated in the same way as biomass) and *L* is the mean carapace length of the females.

Results and Discussion

The standard Ricker stock-recruitment fits are shown in Fig. 4 and 5. The biomass of mature females explained only less than 10% of the observed variation in recruitment with the coefficients of the density-independent and the density-dependent terms amounting to 0.171 and 0.005, respectively. The stock recruitment fit improved slightly using potential egg production. In this case 18 % of the recruitment variability were explained and the coefficients of the density-independent and the density-dependent terms amounted to 0.882 and 0.024, respectively.

Significant variables in the multiple regression models were bottom temperature in the year of larval settling, mean female length and biomass of Greenland halibut in the year before the age 2 recruits were recorded in the survey, and explained 89 and 90% of the recruitment variability together either with the biomass of mature females or egg production as the measure of parental stock size. The coefficients bottom temperature and mean female size were positive and negative for Greenland halibut biomass in both cases (Table 1a). This is plausible considering that a higher temperature can enhance growth if food is not limiting, fecundity is positively correlated with size and an increase in Greenland halibut biomass would reduce recruitment due to predation. Mean female length was also significant when egg production was used as the measure of parent stock size, and this may indicate that either the fecundity-length relationships from the Barents Sea are not adequate for West Greenland or that female size has an additional effect, e.g. on egg quality. It is noteworthy that cod had obviously not effect on the recruitment of northern shrimp in the past decade, but this will likely change if the cod stock does recover from its current low level.

Bottom temperature was the only variable that remained significant when cod and Greenland halibut biomass were removed from the set of initial explanatory variables and parental stock size was forced into the models (Table 1b). These models have more degrees of freedom than those, which include all significant variables, but the explained variability in recruitment decreased to 46% using biomass of mature females as measure of the parental stock and to 40% with potential egg production instead.

Figure 6 compares the predictions of recruitment from the standard Ricker and the multiple regression models. The two standard Ricker models, which were either based on biomass of mature females (Fig. 6A) or potential egg production (Fig. 6B), predict a moderate increase in recruitment above the long-term mean (9.4×10^9) in the coming years despite the substantial increase of females biomass from 152 000 tons in 2002 to the record high value of 264 000 tons in 2004 (Fig. 1) In contrast, the multiple regression models with the full set of significant variables or the reduced one suggest a drastic decline of recruitment in 2005 or in 2006, respectively. Although these models represent the observations from the past years fairly well, it appears questionable that the magnitude of the predicted decline in recruitment is realistic even considering the pronounced changes in Greenland halibut biomass and mean females size (Fig. 1) in the first case and the decrease in bottom temperature (Fig. 1) in both cases since 2001.

Conclusions

The proportion of mature females calculated from Icelandic data on temperature-specific maturation (Skúladóttir *et al.*, 1991) and bottom temperatures recorded off West Greenland ranged from 81.8 to 93.4% (at temperatures of 1.5 and 3.4°C, respectively) and had only a minor effect on index of spawning stock biomass used in this study. These values, however, are above those reported by Horsted (1978) for the 1950s and 1970s. It appears therefore worthwhile to collect more recent information on the portion of egg bearing females, e.g. from the commercial shrimp fishery in winter as such data cannot be derived from the West Greenland Bottom Trawl survey for shrimp because this survey is conducted prior or in the beginning of the egg laying period.

Folmer (1990) reported that individual fecundity of northern shrimp females at West Greenland was much lower in areas north of 71°N than in the Holsteinsborg Deep at about 66°30'N where usually higher temperatures prevail (Wieland and Kanneworff, 2002). This may justify the approach used here to calculate the potential egg production applying two different levels of fecundity for northern shrimp in the Barents Sea, but it would be highly desirable to collect more adequate data on the effect of temperature on fecundity for the West Greenland stock.

Northern shrimp is not fully represented in the survey at age 2 (Wieland, 2004b). This effect and missing observations at low sizes of the parental stock have prevented a more realistic fit of the standard Ricker function near the origin. A scaling of the recruitment index with a constant factor, however, would not improve the fit or change the value of density-dependent term. Berenboim and Sheveleva (1989) reported for northern shrimp in the Barents an egg mortality of about 37% during the 5 month long egg bearing period, and improved stock recruitment fits might be obtained if the measure of parental stock size is adjusted taking such an effect into account. This, however, would require a collection of more detailed information on the duration of the egg bearing period and egg mortality during this period in relation to temperature for West Greenland waters.

The years available for the time series of stock-recruitment data do so far not include situations of low parental stock size and observations of the outcome from the record high levels of female biomass in 2003 and 2004 are outstanding. The predictions from the standard Ricker models should be taken with much caution considering that data from the coming years will likely modify the shape of the stock-recruitment relationship. This is also the case for the multiple regression models, in particular those that were derived from the full initial set of explanatory variables, because they were based on low degrees of freedom fitting four variables with only 12 observations. New data may alter the significance of one or the other environmental factor and the corresponding coefficients. However, the results of this study suggest that recruitment in the near future will be at or even below the average of the last three years despite the high level of female biomass.

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Table 1. Parameter estimates of multiple regressions models on recruitment of northern shrimp in West Greenland waters, 1993-2004 (*: variable forced into the model).

a) with cod and Greenland halibut biomass in the initial set of explanatory variables

Variable	Coefficient	P		Variable	Coefficient	P	
(Intercept)	-67.1254	0.0009		(Intercept)	-66.5260	0.0007	
Biomass of mature females and	0.0304	0.0135		Potential egg production and	0.1871	0.0080	
Mean female size of northern shrimp	2.3905	0.0012		Mean female size of northern shrimp	2.4789	0.0008	
Bottom temperature	1.4109	0.0001		Bottom temperature	1.0016	0.0003	
Biomass of Greenland halibut	-0.1222	0.0019		Biomass of Greenland halibut		0.0010	
R^2:	0.8948			R^2:	0.8982		

b) without cod and Greenland halibut biomass in the initial set of explanatory variables

Variable	Coefficient	P		Variable	Coefficient	P	
(Intercept)	-2.9846	0.0019		(Intercept)	-1.2893	0.0471	
Biomass of mature females of northern shrimp	-0.0137	0.1500	*	Potential egg production of northern shrimp	-0.0826	0.1022	*
Bottom temperature	0.7101			Bottom temperature	0.7675	0.0356	
R^2:	0.4570			R^2:	0.4041		

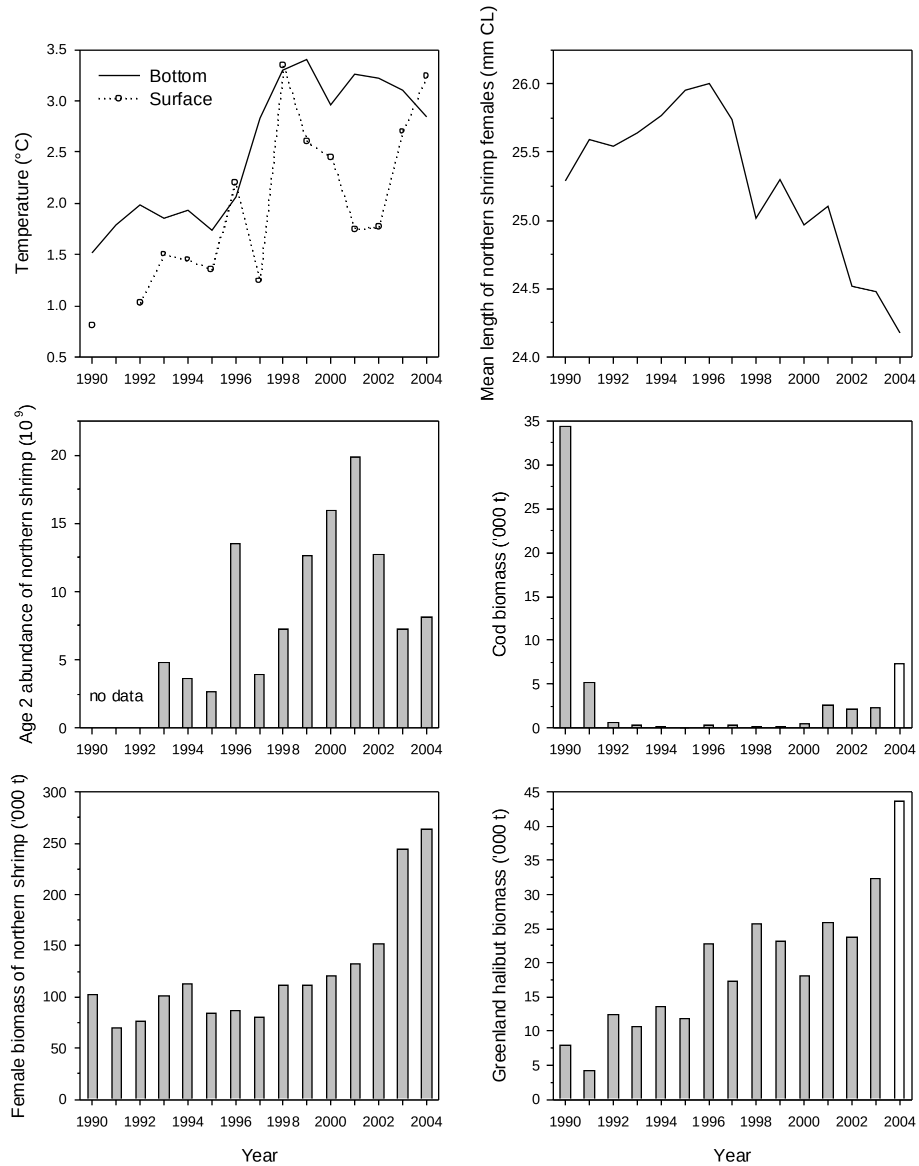

Fig. 1. Time series of bottom and surface temperature, recruitment at age 2, mean length and female biomass of northern shrimp as well as cod and Greenland halibut biomass off West Greenland (Survey indices of cod and Greenland halibut biomass for 2004 are preliminary estimates, see text for references).

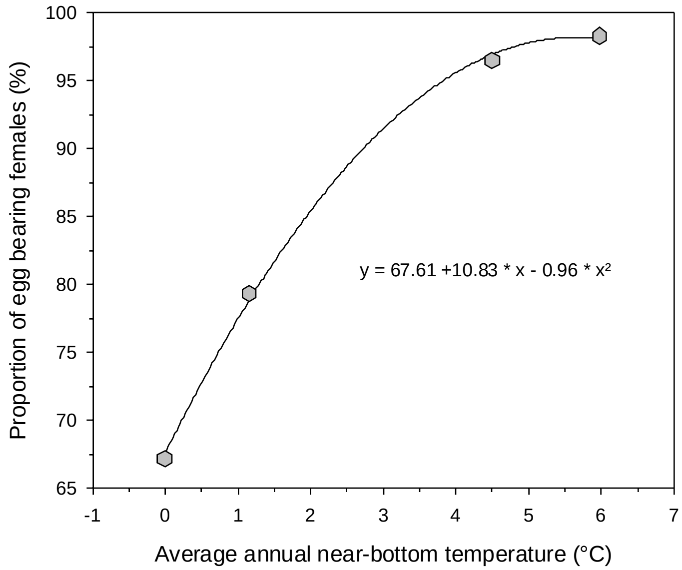

Fig. 2. Proportion of egg bearing females of northern shrimp in December in relation to bottom temperature in two inshore and two offshore areas at Iceland (based on Skúladóttir *et al*., 1991)

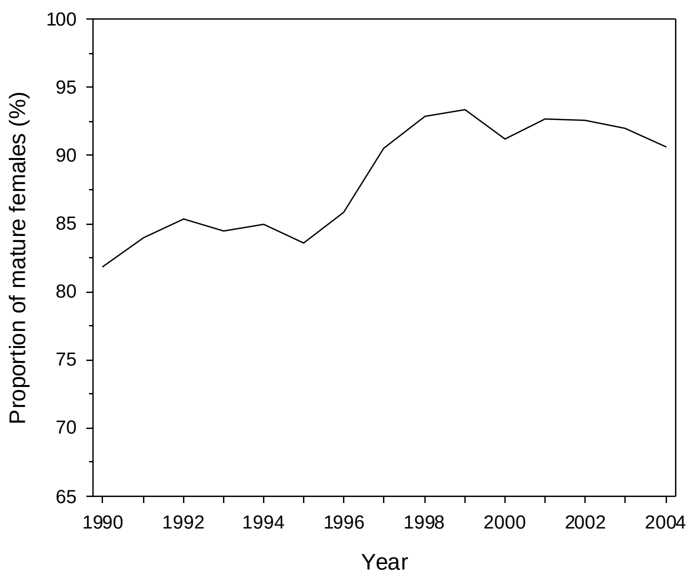

Fig. 3. Estimated proportion of mature females of northern shrimp in West Greenland waters, 1990-2004.

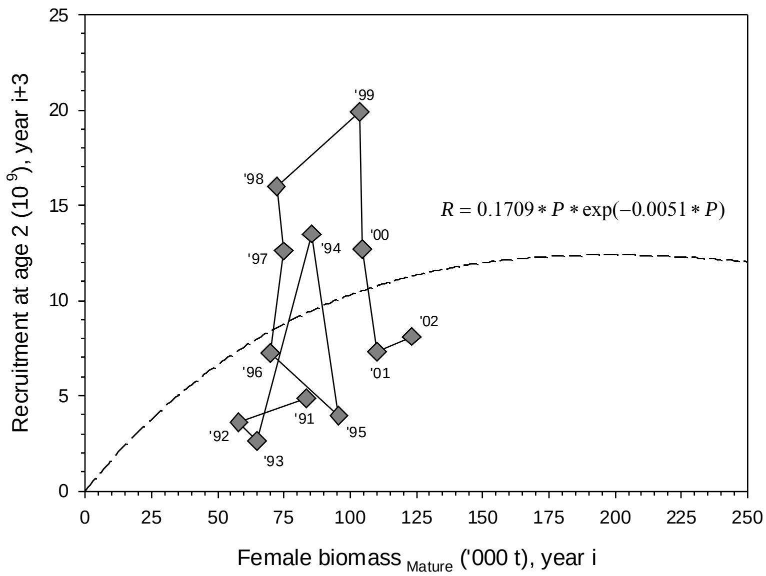

Fig. 4. Stock-recruitment plot for northern shrimp off West Greenland with fitted standard Ricker curve using biomass of mature females as measure of the parental stock (numbers at symbols refer to year-classes).

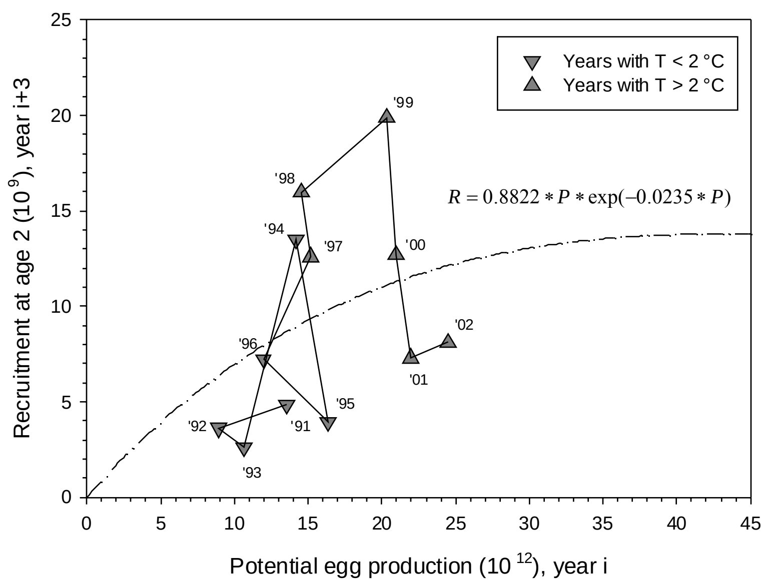

Fig. 5. Stock-recruitment plot for northern shrimp off West Greenland with fitted standard Ricker curve using potential egg production as measure of the parental stock (numbers at symbols refer to year-classes).

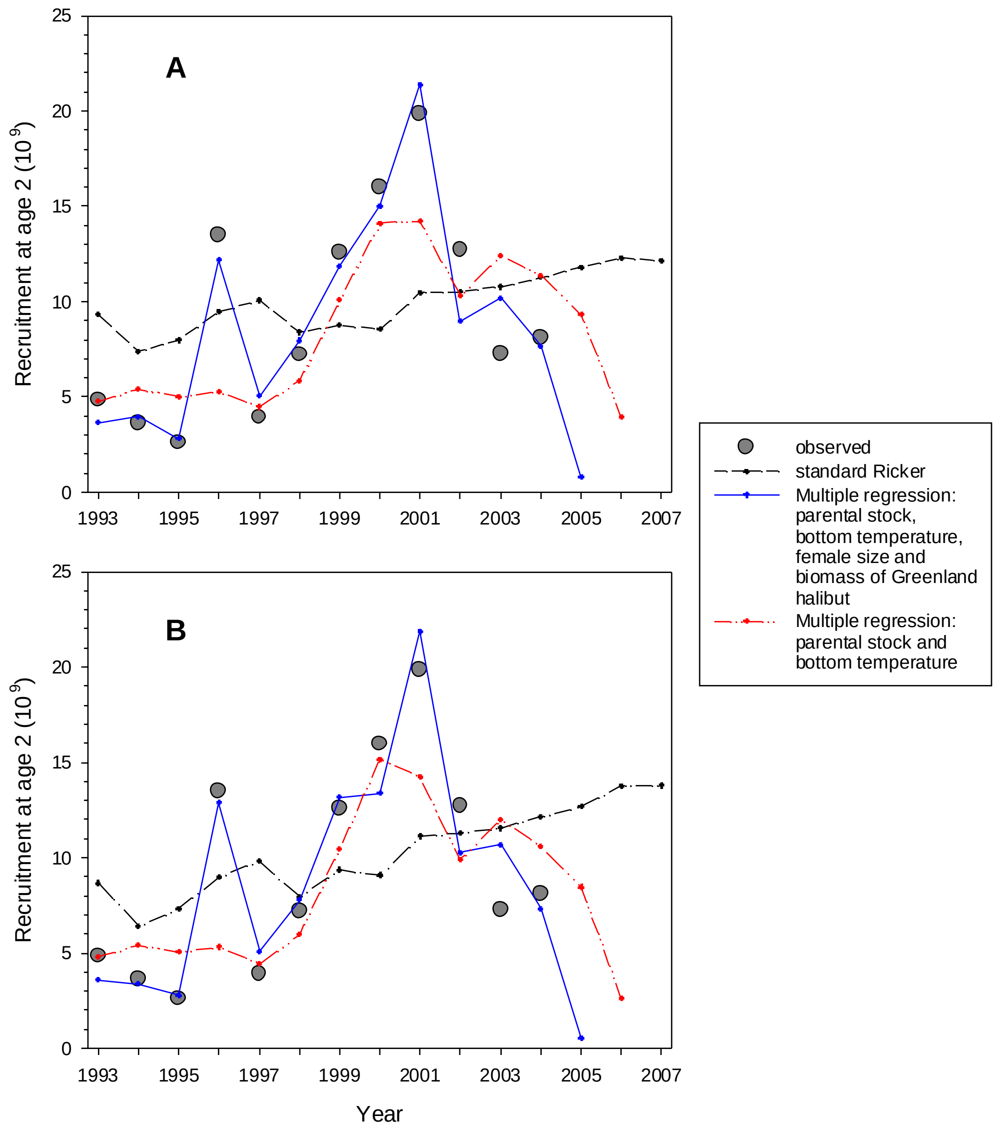

Fig. 6. Comparison of standard Ricker and multiple regression models for the prediction of northern shrimp recruitment at age 2 off West Greenland with biomass of mature females (A) or potential egg production (B) as measure of the parental stock.